

## **Fungal biomass and fungal immobilization of plants nutrients in Swedish coniferous forest soils**

BY

**E. BÅÅTH and B. SÖDERSTRÖM**

*University of Lund, Department of Microbial Ecology, Ecology Building  
Helgonavägen 5, S-223 62 Lund, Sweden*

### **INTRODUCTION**

A considerable part of the potential plant nutrients in soil may be more or less firmly bound in live and dead soil organisms. These immobilized nutrients are thus temporarily withdrawn from uptake by plant roots. By death, lysis, and decomposition, nutrients are released and utilized by roots and living soil organisms.

Fungi usually have the greatest biomass of the organisms in most soils, for example temperate coniferous forest soils. The fungi not only are important as decomposers in these ecosystems, but they also serve as food for part of the soil fauna and are important immobilizers of plant nutrients. Swedish coniferous forest soils are often deficient in nitrogen, and N circulation is thus of great importance for primary production. The study of soil fungal biomass and its immobilizing potential is therefore important not only to the soil microbiologist, but also to zoologists and botanists.

Fungal species composition, the length of fungal mycelia and spatial and seasonal variation are often sufficient information for the soil microbiologist. However, if data on hyphal lengths are to be used in broader ecosystem analyses, the data should be converted to biomass. The aims of the present investigation were thus not only to study total fungal length in different forest soils in Sweden, but also to calculate fungal biomass. In addition, fungal content of carbon, nitrogen, phosphorus and potassium was estimated and compared to the total amounts of these nutrients in the soil.

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## I. — SITES

### *Ivantjärnsheden, Jädraås.*

Ivantjärnsheden, the main field site of the Swedish Coniferous Forest Project, is situated near Jädraås in the province of Gästrikland (60° 49' N, 16° 30' E). The soil is a well-developed iron podzol on a glaci-fluvial sandy sediment. Samples were taken in 4 areas designated Ih O, Ih I, Ih II, and Ih VA. Ih O and Ih VA are mature (120-year old) Scots pine (*Pinus silvestris* L.) stands, while Ih II contains young (20-year old) Scots pine. Ih I was clear-cut in 1967, and slow reforestation has left part of the area completely free from trees. The ground vegetation of all the areas is a dry dwarf type (*Calluna vulgaris* (L.) Hull, *Cladonia* spp.). The annual mean temperature is 3.8° C, and mean yearly precipitation is 607 mm.

### *Nickobacken, Siljansfors.*

The site is situated in the province of Dalarna, central Sweden (60° 55' N, 14° 23' E). It is one of the field sites of the Swedish Coniferous Forest Project. The forest consists mainly of Norway spruce (*Picea abies* (L.) Karst) and Scots pine, with an undervegetation dominated by *Hylocomium splendens* (Hedw.) B.S.G. and *Vaccinium myrtillus* L.. The soil is a morainic iron podzol. The annual mean temperature is 3.6° C, and the mean precipitation is 691 mm per year.

### *Kongalund.*

The site is situated in the province of Skåne, south Sweden, (55° 59' N, 13° 10' E) and is a ca 60-year old Norway spruce forest planted on a former beech forest. Ground vegetation is very sparse. The former mull is now undergoing conversion into podzol, making the deeper horizons A<sub>1</sub>/A<sub>2</sub> and (B) somewhat atypical and not fully comparable with mineral layers at the other sites. In spite of this they will be designated A<sub>2</sub> and B. The annual mean temperature is 6-7° C, and precipitation is 800 mm per year. The site is described in more detail by NIHLGÅRD (1971, 1972) and SÖDERSTRÖM (1975).

### *Norrliden.*

The site is situated in the province of Västerbotten, in northern Sweden (64° 21' N, 19° 46' E). The forest was planted with Scots pine in 1953. The textural soil type is till with a distinctly-developed iron podzol. The annual mean temperature is 1.2° C, and the annual mean precipitation is about 600 mm.

## II. — MATERIAL AND METHODS

### **Sampling methods.**

Soil cores were taken with a stainless steel borer (6 cm diam.). Subsamples from the different horizons were generally pooled to form bulk samples. The horizons sampled were A<sub>00</sub> (L), A<sub>01</sub> (F), A<sub>02</sub> (H), A<sub>2</sub> (E) and the upper 10 cm of B, where A<sub>02</sub> was defined as the lowest 1 cm of the organic layer between A<sub>00</sub> and the bleached layer (A<sub>2</sub>). At some sites A<sub>01</sub> and A<sub>02</sub> were not separated. Roots thicker than 1 mm were removed before further processing. Only conifer needles were used for measurements in the A<sub>00</sub> layer.

The samples were collected as follows: Ivantjärnsheden, Ih O, 1 sampling (23 Sept. 1975), 6 cores taken randomly, not treated as a bulk sample. Ih I, 1 sampling (13 Sept. 1977), 6 cores taken randomly. Ih II, 1 sampling (8 Aug. 1974), 6 cores taken randomly. Ih VA, 6 samplings (26 Sept. 1973, 21 May 1974, 20 Aug. 1974, 20 Nov. 1974, 20 Febr. 1975, 27 May 1975), 6 cores taken on each sampling occasion. Nickobacken, 1 sampling (20 May 1975), 10 cores taken randomly from the dryer area of the site. Kongalund, 2 samplings (20 July 1972, 22 Jan. 1973) each with 10 randomly taken cores. Norrliden, 1 sampling (5 Oct. 1976), 5 cores in each of 3 plots.

### Soil characteristics.

Dry weight of soil was determined by drying at 105° C overnight, and organic matter content was estimated as the weight lost on ignition at 850° C (3 parallels). pH was determined in water (ratio soil: water 1:2). Some characteristics of the different soil layers are given in Table I.

TAB. I

Soil horizon characteristics at 7 Swedish coniferous forest sites  
(LOI = loss on ignition, n. d. = not determined)

Soil horizon	Ih O		Ih I		Ih II		Ih VA		Nickobacken		Kongalund		Norrliden	
	pH	% LOI	pH	% LOI	pH	% LOI	pH	% LOI	pH	% LOI	pH	% LOI	pH	% LOI
A <sub>00</sub> .....	n.d.	n.d.	n.d.	n.d.	n.d.	97	n.d.	95	n.d.	98	3.5	90	n.d.	n.d.
A <sub>01</sub> .....	4.2	90	4.2	87	4.2	80	4.0	83	3.8	95	3.4	75	4.6	63
A <sub>02</sub> .....														
A <sub>2</sub> .....	4.5	3	4.9	1	4.9	4	4.3	3	4.3	2	3.5	15	4.7	5
B.....	4.9	4	4.7	6	4.7	5	4.9	4	5.2	13	3.7	9	5.2	4

### Fungal length determinations.

The agar film method (JONES and MOLLISON, 1948) was slightly modified as follows: The soil sample (5-25 g) was homogenized in 250 ml water with a MSE ATO-mix run at 10 000 rpm for 10 min. Studies showed that this dispersion treatment gave optimum hyphal detection in the soil types investigated. The needles from the A<sub>00</sub> layer were cut into 1 mm pieces and macerated in water suspension with a Bühler knife blender at 40 000 rpm for 5 min. After dispersion treatment, heavier particles in the suspensions were allowed to settle for 15 sec. 25 ml of the suspension were then pipetted from 2 cm below the surface and diluted. The last dilution was made with a molten agar solution to a final agar concentration of 2 %. The soil-agar suspension was kept at 50° C on a heated magnetic stirrer, and an agar-film was made in a preheated 0.1 mm deep haemocytometer. After the preparation was dried, it was stained with phenolic aniline blue for one hour and examined under a × 100 immersion oil objective with phase-contrast (total magnification × 800). Hyphae were traced on paper using a camera lucida or measured with the inter section method (OLSON, 1950). Identical results were obtained when these two methods were compared. 4 preparations were made from each sample, and at least 20 fields of view were counted per preparation, giving a standard error for mean counts between 5 and 10 %.

### Fungal biomass and nutrient content.

Fungal biomass was calculated using measured values for hyphal cross section and considering fungal hyphae to be cylinders. The mean hyphal cross section was calculated according to equation (3) in BÄATH and SÖDERSTRÖM (1979). A density of  $1.1 \text{ g cm}^{-3}$  (SAITO, 1955) and an assumed dry weight of 15 % of wet weight were used (DE BOOIS (1976) reported 8-15 % and HANSEN and GOKSØYR (1975) 17 %).

Nutrient content of the mycelia was estimated by growing some common soil fungi (isolated at Ih VA) in soil extract from the  $A_{01}/A_{02}$  horizon for one month and analyzing the mycelia for N, P and K. As % of dry weight the mycelia contained 3.7 % N, 0.7 % P and 1.1 % K (mean values). The growth medium had a C/N ratio of 150. AC content of 45 % of dry weight was used (COCHRANE, 1958).

## III. — RESULTS

Fungal lengths in the soil horizons of the seven sites studied are given in Table II. At all sites the highest values per g dry weight soil were found in the  $A_{01}$  or the  $A_{01}/A_{02}$  horizons, although variation among the

TAB. II

Fungal length in horizons of 7 Swedish coniferous forest soils  
Expressed as m (g dw soil)<sup>-1</sup>. (n.d. = not determined)

Soil horizon	Ih O	Ih I	Ih II	Ih VA	Nickobacken	Kongalund	Norrheden
$A_{00}$ .....	n.d.	n.d.	3 700	5 800	9 700	1 200	n.d.
$A_{01}$ .....	15 200	3 900	12 700	18 700	66 900	2 900	3 700
$A_{02}$ .....			7 000	7 500	37 000	2 400	
$A_2$ .....	1 200	410	540	650	1 500	940	820
B.....	740	350	500	390	2 100	650	140

sites was great. The greatest hyphal length was found at Nickobacken ( $66\,900 \text{ m.g dw}^{-1}$ ), while the lowest value was recorded at Kongalund ( $2\,900 \text{ m.g dw}^{-1}$ ). Low values were found in the mineral horizons, somewhat higher in the  $A_2$  than in the B horizon. In the  $A_2$  horizon fungal lengths ranged between  $410\text{--}1\,500 \text{ m.g dw}^{-1}$  and in the B horizon between  $140\text{--}2\,100 \text{ m.g dw}^{-1}$ .

The soil horizons not only differed in mycelial content, but qualitative differences were also found. The proportion of hyphae with clamp connections was significantly higher ( $p < 0.05$ ) in the  $A_{02}$  horizon than in the other horizons at Ivantjärnsheden, Ih VA. Large differences in hyphal diameter were also found among the soil horizons (Tab. III). For example, hyphal diameter at Ih VA was in  $A_{00}$   $2.7 \mu\text{m}$ ,  $A_{01}$   $2.7 \mu\text{m}$ ,  $A_{02}$   $2.5 \mu\text{m}$  and in  $A_2$  and

B 1.9  $\mu\text{m}$ . This tendency, with thinner hyphae in the mineral layers, was found at all sites except Nickobacken. The overall range of mean hyphal diameter was 1.3-3.0  $\mu\text{m}$ .

TAB. III

Mean diameter of fungal hyphae in horizons of 7 Swedish coniferous forest soils  
Expressed as  $\mu\text{m}$  (SE). (n.d. = not determined)

Soil horizon	Ih O	Ih I	Ih II	Ih VA	Nicko- backen	Konga- lund	Norrleden
A <sub>00</sub> .....	n.d.	n.d.	2.6 (0.1)	2.7 (0.1)	2.7 (0.1)	2.6 (0.1)	n.d.
A <sub>01</sub> .....	2.2 (0.1)	2.3 (0.1)	3.0 (0.2)	2.7 (0.1)	1.9 (0.1)	2.9 (0.2)	1.9 (0.1)
A <sub>02</sub> .....			1.9 (0.1)	2.5 (0.2)	1.7 (0.1)	2.7 (0.1)	
A <sub>2</sub> .....	1.6 (0.1)	1.6 (0.1)	1.6 (0.1)	1.9 (0.2)	2.6 (0.2)	2.6 (0.1)	1.5 (0.1)
B.....	1.4 (0.1)	1.3 (0.1)	2.1 (0.1)	1.9 (0.1)	2.3 (0.2)	2.3 (0.1)	1.7 (0.1)

Fungal biomass in the organic layers ranged from 1.2-35.1 mg dw . g dry soil<sup>-1</sup>, and in the mineral layers 0.1-1.9 mg dw . g dry soil<sup>-1</sup> (Tab. IV). Difference in biomass between the different sites were approximately the same as for fungal length. Differences between the organic and mineral horizons were enhanced with fungal biomass compared to fungal length at all sites except Nickobacken.

TAB. IV

Fungal biomass in horizons of 7 Swedish coniferous forest soils  
Expressed as mg dw (g dw soil)<sup>-1</sup>. (n.d. = not determined)

Soil horizon	Ih O	Ih I	Ih II	Ih VA	Nicko- backen	Konga- lund	Norrleden
A <sub>00</sub> .....	n.d.	n.d.	4.0	6.7	11.2	1.2	n.d.
A <sub>01</sub> .....	11.2	3.0	19.3	21.4	35.1	3.6	2.1
A <sub>02</sub> .....			3.9	7.3	19.5	2.5	
A <sub>2</sub> .....	0.5	0.2	0.2	0.4	1.6	0.9	0.3
B.....	0.2	0.1	0.3	0.2	1.9	0.5	0.1

The biomass at Ih VA was estimated to be 73 g dw per square meter in the top 20 cm of the soil. Of this, 35 g dw (48 %) was found in the mineral horizons (A<sub>2</sub> + B = 15 cm). In Kongalund a fungal biomass of 102 g dw . m<sup>-2</sup> was estimated for the top 15 cm (A<sub>00</sub> horizon excluded). Unfortunately, areal calculations could not be done at the other sites.

An estimation of fungal content of carbon, nitrogen, phosphorus and potassium in Ih VA is presented in Figure 1. The values for the  $A_{00}$  horizon may be underestimated, since fungal biomass was determined in conifer needle litter only.

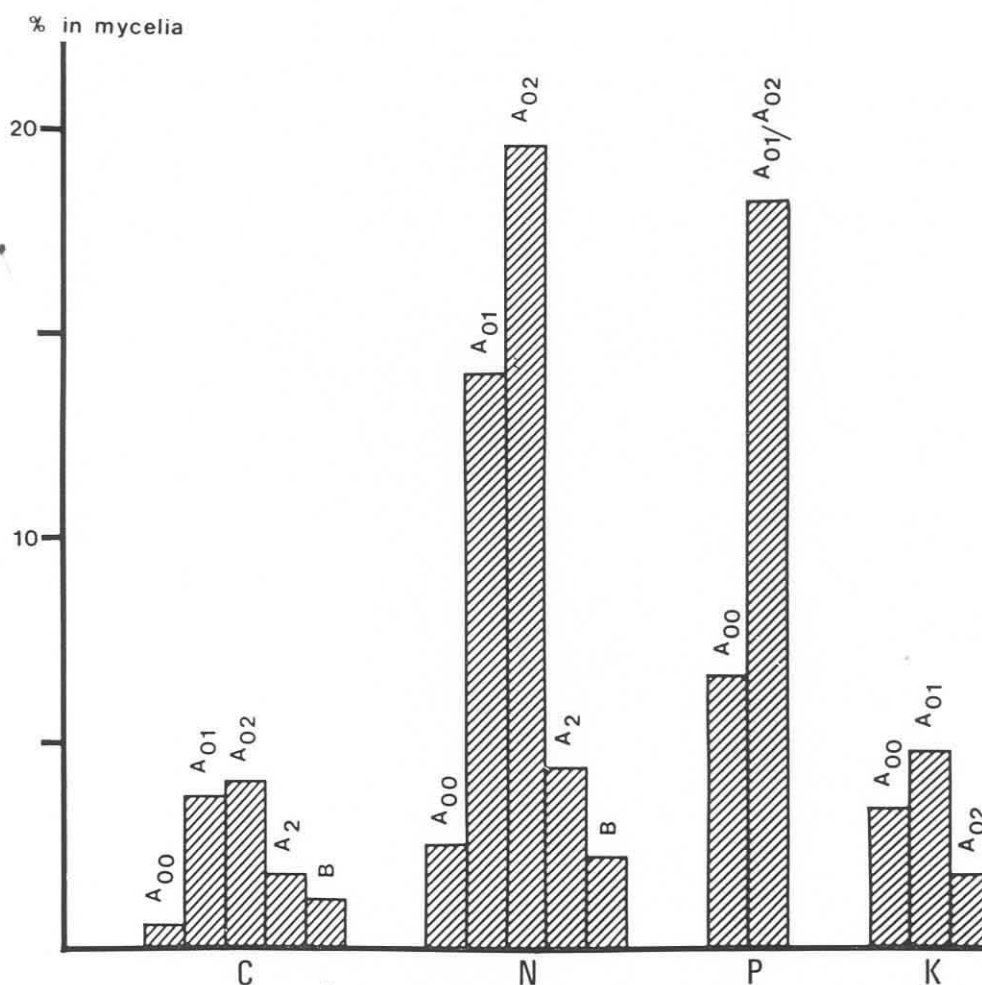


FIG. 1. — C, N, P and K bound in fungal biomass as a percentage of the total amounts in the soil horizons of Ivantjärnsheden, Ih VA.

The fungal carbon content was small in all soil layers, ranging between 0.6 and 4.1 % of the total carbon in the horizons. The proportion of total N bound in fungal biomass was highest in the  $A_{01}$  and  $A_{02}$  horizons, more than 10 %, while values for the other horizons were between 2.2 and 4.4 %. Phosphorus and potassium figures are given only for the organic horizons. In the  $A_{01}/A_{02}$  horizon almost 20 % of the total P was found in fungal mycelia, while lower values were recorded in the litter layer ( $A_{00}$ ). The highest value for K, 4.8 %, was recorded in the  $A_{01}$  horizon. In all 33 g C m<sup>-2</sup> was estimated to be bound in fungal mycelia. Corresponding values for the other elements were: N 2.7 g m<sup>-2</sup>, P 0.5 g m<sup>-2</sup>, K 0.8 g m<sup>-2</sup>.

At Kongalund it was possible to estimate fungal immobilization of carbon and nitrogen using values from NIHLGÅRD (1971) for the total amount in the soil. Fungal immobilization in the top 15 cm was considerably smaller here

compared with Ih VA. Of the total carbon, fungal hyphae were estimated to contain 0.9 %. The figure for nitrogen was somewhat higher, 1.4 %. In this area there appeared to be no increased immobilization in the  $A_{01}/A_{02}$  horizon. In all, 46 g C.m<sup>-2</sup> and 3.8 g N.m<sup>-2</sup> were estimated to be immobilized by the soil fungi.

#### IV. — DISCUSSION

NICHOLAS and PARKINSON (1967) compared four different methods to measure soil hyphae and concluded « that the agar film technique proved the best method for accurate, absolute, quantitative assessments of amounts of mycelium in soil ». It has been claimed that phenolic aniline blue stained hyphae can be considered live (NAGEL-DE BOOIS and JANSEN, 1976), but others have rejected this (PARKINSON *et al.*, 1971, SKINNER *et al.*, 1952). FRANKLAND (1975) described a method to estimate the living fraction of the biomass counted on agar film, but her method has not been used in this study. Thus, the agar-film method as applied here tells little about fungal activity in the soil.

It is difficult to interpret seasonal biomass variations in terms of changes in fungal activity, as these variations can be due to changes in the decomposition rate of dead fungal hyphae. Varying biomass was found on the different sampling occasions in the Ih VA area, but these changes did not follow a consistent seasonal pattern, and they could not be related to any other measured parameter (e.g. temperature, soil moisture content, litter fall). Therefore, only the means are presented in Table II.

The mycelial lengths given in Table II are fairly large, especially at Ivantjärnsheden and Nickobacken, compared to other studies from temperate and arctic forest sites (e.g. HANSSEN and GOKSØYR, 1975, NAGEL-DE BOOIS and JANSEN, 1971, VISSER and PARKINSON, 1975, WIDDEN and PARKINSON, 1973). Direct comparisons of the results of different workers are, however, hazardous. The horizons may be sampled in different ways, preparation procedures may be different and the microscopic countings may be performed differently (e.g. different magnification or the use of phase contrast optics). Nevertheless, the large difference in mycelial length between Nickobacken and Ivantjärnsheden on the one hand and most other sites on the other seems to justify the conclusion that the soil mycelial content at these two Swedish sites is extraordinarily high.

In the present study, total mycelial length differed considerably among the 7 sites studied. One explanation for these differences could be the different stand ages. A comparison between the  $A_{01}/A_{02}$  horizons in the 4 pine forests studied at Jädraås reveals that greatest mycelial lengths were found in the mature forests (Ih VA and Ih O), and the lowest values in the clear-cut area (Ih I). The 20-year old forest (Ih II) had total mycelial lengths between these two extremes. Thus, clear-cutting may have resulted in a decreased soil mycelium content and a subsequent release of mineral nutrients. During reforestation the total amount of fungal mycelia in the soil, and thus the nutrients bound in soil hyphae, appeared to increase. This hypothesis may

also explain the rather low values for Norrliden, which is a fairly young forest. More data must be obtained to evaluate this hypothesis.

If biomass values (Tab. IV) are compared these hypothetical differences due to stand age are less pronounced. The 20 year old stand, Ih II, had a fungal biomass in the  $A_{01}/A_{02}$  horizon that was between that in the two mature stands, Ih O and Ih VA.

There are remarkably few reports on soil fungal biomass per unit area in other forest sites. Expressing biomass on a  $m^2$  basis is often ecologically more meaningful, if e.g. a comparison with the energy input at a site is to be made. FLANAGAN and VAN CLEVE (1977) found  $4.8 \text{ g dw} \cdot m^{-2}$  in the top 20 cm of a black spruce forest soil on permafrost in Alaska, and a deciduous forest soil in England contained  $45.4 \text{ g dw} \cdot m^{-2}$  (GRAY and WILLIAMS, 1971). VISSER and PARKINSON (1975) reported a biomass of  $291 \text{ g ww} \cdot m^{-2}$  in October in the organic layers (less than 10 cm thick) of a Canadian aspen poplar (*Populus tremuloides* Michx.) forest. Using a dry weight of 15 % of wet weight, this biomass corresponds to  $44 \text{ g dw} \cdot m^{-2}$ . PARKINSON *et al.* (1978) found an average yearly live fungal biomass of  $7.4 \text{ g C} \cdot m^{-2}$  in the organic soil layers. Assuming 45 % C of dry weight, this biomass corresponds to  $16.4 \text{ g dw} \cdot m^{-2}$ . In the organic horizons of Ivantjärnsheden, Ih VA, we recorded a fungal biomass of  $38 \text{ g dw} \cdot m^{-2}$ . Thus, fungal biomass  $m^{-2}$  at the Swedish sites is high, but not exceptionally high.

The importance of expressing biomass values on a  $m^2$  basis is further demonstrated by comparing Ih VA and Kongalund. Although Kongalund had a much lower mycelial content per g dry weight soil, the fungal biomass  $m^{-2}$  was higher than that at Ih VA.

BÄATH and SÖDERSTRÖM (1979) described three equations used to calculate the average cross section of fungal hyphae, and they pointed out that the choice of calculation method strongly influences the estimated biomass. In the present study, we have used equation (3). If equation (2) is used instead values 7.7-29 % lower than those in Table IV are obtained. The use of equation (4) in Ih VA and Ih II would result in values 86-140 % of those given in Table IV.

As the width of the hyphae strongly influences the volume and biomass of soil fungi, thick hyphae, although less numerous, could account for most of the biomass, especially in the mineral soil. This was not the case, however, as illustrated in Figure 2. In the mineral soil thinner hyphae accounted for the greater part of the biovolume. Hyphae thinner than  $3 \mu m$  made up 16, 26, 25, 63 and 68 % of the total biovolume in the horizons  $A_{00}$ ,  $A_{01}$ ,  $A_{02}$ ,  $A_2$  and B, respectively.

A large part of the hyphae counted with the agar-film method at these Swedish sites were probably dead or inactive. Three factors support this assumption. First, for some of the research areas the percentage of phenolic aniline blue-stained hyphae was measured. The values ranged between 10-22 % at Ivantjärnsheden, Ih II and Ih VA, 1-10 % at Nickobacken and 25-53 % at Kongalund. As stated above, blue-stained hyphae are not equivalent to living hyphae but this staining may still give a better idea of the order of magnitude of living mycelia. Second, the energy reaching the soil through litter fall and root death is not enough to maintain this much fungal myce-

lium in soil if all of it was living and metabolizing. Using the model of MARR *et al.* (1963), with values for maintenance demand and yield coefficient from FLANAGAN and BUNELL (1976), it is possible to estimate the substrate needed for maintenance of the fungal biomass. At Ivantjärnsheden, Ih VA, more energy than the total litter input (litter fall and root death) is needed,

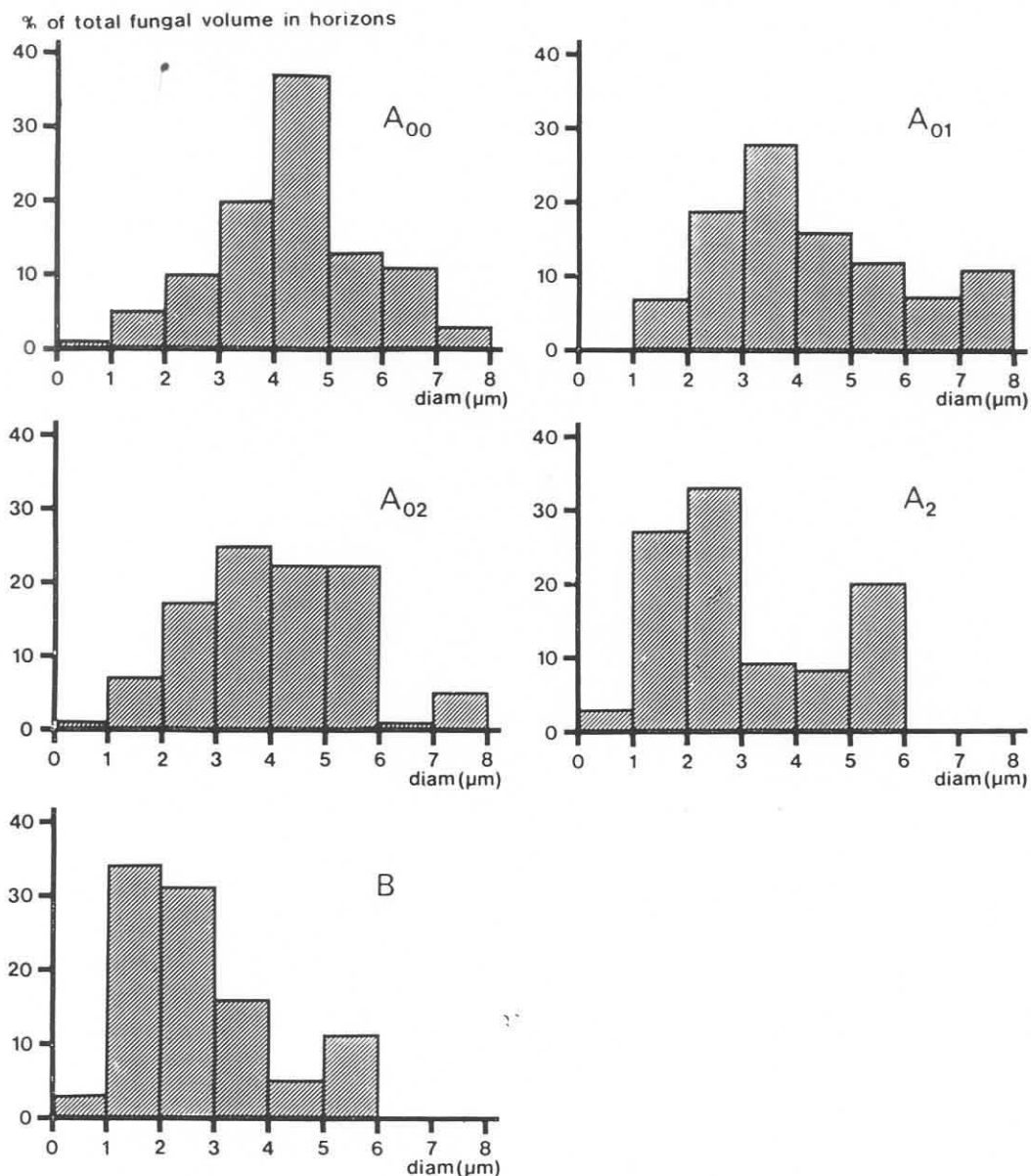


FIG. 2. — Contributions of hyphae of different diameter classes to the total fungal biovolume in 5 horizons at Ivantjärnsheden, Ih VA. Calculated as percentages of the total biovolume in each horizon.

and at Kongalund more than the litter fall is needed. Data on litter production were taken from STAFF and BERG (1977) and NIHLGÅRD (1972). Third, SÖDERSTRÖM (1979 b), using a fluorescence method, found only 1.5 % of the hyphae counted with the agar-film method to be active. Although these values probably are underestimates (SÖDERSTRÖM, 1979 a), they indicate that a large part of the hyphae in the soils studied by us was dead or inactive.

Using values for fungal biomass, it is possible to estimate the retention of mineral nutrients in fungi, provided that the chemical composition of soil mycelia is known. The chemical composition of soil hyphae is difficult to estimate, however, as collecting mycelia free from contaminating soil in quantities large enough to permit chemical analysis is very difficult. Most studies on chemical composition of fungi have dealt with pure culture systems which are difficult to relate to conditions prevailing in soil. Furthermore, different growth media and species and age of mycelia may influence chemical composition. This explains the range of values given in the literature e.g. for nitrogen content, 2.3-68.5 mg.g dw<sup>-1</sup> (MERILL and COWLING, 1966; SWIFT, 1973; AUSMUS *et al.*, 1976; FLANAGAN and VAN CLEVE, 1977; FRANKLAND *et al.*, 1978). The values used in this report to calculate fungal immobilization of nutrients are within the range of values given in literature.

In a black spruce taiga ecosystem, the estimated mean soil fungal immobilization was 0.3 % for N and 0.4 % for P (calculated from FLANAGAN and VAN CLEVE (1977) as percentage of the total nutrient content of the soil). In the organic horizons of a spruce forest in Germany 0.2-0.9 % C and 0.5-2.8 % N were found in fungal mycelia (calculated from PARKINSON *et al.* (1978)). This is lower than the estimates in the present study. AUSMUS *et al.* (1976), on the other hand, found a greater immobilization in a mesic hardwood forest in U.S.A. However, both bacteria and fungi were included in their calculations, and great variations were recorded during the year. This makes direct comparison with our results difficult.

Comparison of the immobilization estimates from these studies shows considerable differences in the amount of a nutrient bound in fungal biomass when calculated as a percentage of the total amount in the soil. Furthermore, relative immobilization among the soil horizons appears to differ in different soils. The reason for these differences is difficult to elucidate, as very little data exist. This fact urges further detailed studies on soil microbial biomass and immobilization.

FRANKLAND *et al.* (1978) stated that the conversion factors used in the calculations of biomass from fungal biovolume are « as important as that of the primary measurements ». Throughout this study, we have used 85 % water content of hyphae and a wet-weight specific gravity of 1.1. These values may underestimate the fungal biomass. In a recent investigation, VAN VEEN and PAUL (1979) determined the ratio between dry weight and wet volume for different fungi subjected to different moisture stresses. They suggested a conversion factor of 0.33 g cm<sup>-3</sup>. The use of their factor would double all biomass values given in Table IV, as well as the values given for fungal immobilization of C, N, P and K.

#### ACKNOWLEDGEMENTS

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## SUMMARY

Fungal length and biomass were studied in horizons of seven Swedish coniferous forest soils with the agar-film method. Both hyphal length and biomass ( $\text{g dw}^{-1}$ ) were greatest in the  $A_{01}$  or the  $A_{01}/A_{02}$  horizons at all sites. The range in hyphal length in the organic horizons was 1 200-66 900  $\text{m} \cdot \text{g dw}^{-1}$  and in the mineral horizons 140-2 100  $\text{m} \cdot \text{g dw}^{-1}$ . Mean hyphal diameter differed in the different horizons; hyphae in the organic soil layers varied between 1.7-3.0  $\mu\text{m}$  in diameter, while in the mineral horizons the range was 1.3-2.6  $\mu\text{m}$ . Fungal biomass was estimated to 73  $\text{g dw} \cdot \text{m}^{-2}$ , 0-20 cm soil depth and 102  $\text{g dw} \cdot \text{m}^{-2}$ , 0-15 cm, at two of the sites. Immobilization of C, N, P and K in soil hyphae was also estimated in one of the soils. Hyphal content expressed as a percentage of the total amount in the soil was for C 0.6-4.1 %, for N 2.2-19.6 %, for P 6.7-18.2 % and for K 1.8-4.8 %.

## ZUSAMMENFASSUNG

Pilzliche Biomasse und Mycellänge wurden in Horizonten von 7 schwedischen Nadelwaldböden mit der Agarfilm-Methode untersucht. Die größte Biomasse und Mycellänge ( $\text{TG}^{-1}$ ) wurden in der F- oder F/H-Schicht in allen Versuchsflächen gefunden. Die Mycellänge in den organischen Horizonten lag zwischen 1 200 und 66 900  $\text{m} \cdot \text{TG}^{-1}$ . Der Hyphendurchmesser war in verschiedenen Schichten variierend. In den organischen Horizonten lag der Durchmesser zwischen 1.7 und 3.0  $\mu\text{m}$ , und in den Mineralbodenschichten zwischen 1.3 und 2.6  $\mu\text{m}$ . Die pilzliche Biomasse wurde zu 73  $\text{g TG} \cdot \text{m}^{-2}$  (0-20 cm) und 102  $\text{g TG} \cdot \text{m}^{-2}$  (0-15 cm) in zwei von den Versuchsflächen errechnet. Der Inhalt von C, N, P und K im Pilzmycel wurde in einer der Versuchsflächen errechnet. In Prozent vom Inhalt des Bodens enthielt das Mycel 0.6-4.1 % C, 2.2-19.6 % N, 6.7-18.2 % P und 1.8-4.8 % K.

## RÉSUMÉ

Nous avons étudié la longueur fongique et la biomasse dans différents horizons de sol de sept forêts de conifères en Suède. La longueur hyphale ainsi que la biomasse ( $\text{g sol}^{-1}$ ) ont atteint un maximum dans les horizons  $A_{01}$  et  $A_{01}/A_{02}$  dans toutes les localités. La longueur hyphale totale a démontré une variation entre 1 200 et 66 900  $\text{m} \cdot \text{g sol}^{-1}$  dans les horizons organiques et entre 140 et 2 100  $\text{m} \cdot \text{g sol}^{-1}$  dans les couches minérales. Le diamètre hyphal moyen se montre différent dans les différents horizons : dans les couches organiques entre 1,7 et 3,0  $\mu\text{m}$  et dans les horizons minéraux entre 1,3 et 2,6  $\mu\text{m}$ . La biomasse fongique a été évaluée à 73  $\text{g} \cdot \text{m}^{-2}$  dans une profondeur de sol de 0-20 cm et à 102  $\text{g} \cdot \text{m}^{-2}$  dans une profondeur de 0-15 cm, en deux localités. Nous avons aussi estimé l'immobilisation de C, N, P et K dans les hyphes de sol dans une des localités et trouvé un contenu dans les hyphes (exprimé en pourcent de la quantité totale dans le sol) en C de 0,6-4,1 %, en N de 2,2-19,6 %, en P de 6,7-18,2 % et en K de 1,8-4,8 %.

## REFERENCES

- AUSMUS (B. S.), EDWARDS (N. T.) and WITKAMP (M.), 1976. — Microbial immobilization of carbon, nitrogen, phosphorus and potassium: implications for forest ecosystem processes. In: *The role of terrestrial and aquatic organisms in decomposition processes*. (Ed. ANDERSON (J. M.) and MACFADYEN (A.)). Blackwell Scientific Publications, Oxford, pp. 397-416.

- BAATH (E.) and SÖDERSTRÖM (B.), 1979. — The significance of hyphal diameter in calculation of fungal biovolume. *Oikos*, **33**: 11-14.
- BOOIS (H.M.) de, 1976. — Fungal development on oak leaf litter and decomposition potentialities of some fungal species. *Rev. Ecol. Biol. Sol*, **13**: 437-448.
- COCHRANE (V.W.), 1958. — *Physiology of fungi*. John Wiley & Sons, Inc. New York, 524 p.
- FLANAGAN (P.W.) and BUNNELL (F.C.), 1976. — Decomposition models based on climatic variables, substrate variables, microbial respiration and production. In: *The role of terrestrial and aquatic organisms in decomposition processes*. (Ed. ANDERSON (J.M.) and MACFADYEN (A.)). Blackwell Scientific Publications, Oxford, pp. 437-457.
- FLANAGAN (P.W.) and VAN CLEVE (K.), 1977. — Microbial biomass, respiration and nutrient cycling in a black spruce taiga ecosystem. In: *Soil organisms as components of ecosystems*. (Ed. LOHM (U.) and PERSSON (T.)). *Proc. 6th Int. Coll. Soil Zool., Ecol. Bull.* (Stockholm), **25**: 261-273.
- FRANKLAND (J.C.), 1975. — Estimation of live fungal biomass. *Soil Biol. Biochem.*, **7**: 339-340.
- FRANKLAND (J.C.), LINDLEY (D.K.) and SWIFT (M.J.), 1978. — A comparison of two methods for the estimation of mycelial biomass in leaf litter. *Soil Biol. Biochem.*, **10**: 323-333.
- GRAY (T.R.G.) and WILLIAMS (S.T.), 1971. — Microbial productivity in soil. *Symp. Soc. Gen. Microbiol.*, **21**: 255-286.
- HANSEN (J.F.) and GOKSØYR (J.), 1975. — Biomass and production of soil and litter fungi at Scandinavian tundra sites. In: *Fennoscandian tundra ecosystems. I. Plants and microorganisms*. (Ed. WIELGOLASKI (F.E.)). Springer, Berlin-Heidelberg-New York, pp. 239-243.
- JONES (P.C.T.) and MOLLISON (J.E.), 1948. — A technique for the quantitative estimation of soil micro-organisms. *J. gen. Microbiol.*, **2**: 54-69.
- MARR (A.G.), NELSON (E.H.) and CLARK (D.J.), 1963. — The maintenance requirements of *Escherichia coli*. *Ann. N.Y. Acad. Sci.*, **102**: 536-548.
- MERRILL (W.) and COWLING (E.B.), 1966. — Role of nitrogen in wood deterioration: amount and distribution of nitrogen in fungi. *Phytopath.*, **56**: 1083-1090.
- NAGEL-DE BOOIS (H.M.) and JANSEN (E.), 1971. — The growth of fungal mycelium in forest soil layers. *Rev. Ecol. Biol. Sol*, **8**: 509-520.
- NICHOLAS (D.P.) and PARKINSON (D.), 1967. — A comparison of methods for assessing the amount of fungal mycelium in soil samples. *Pedobiol.*, **7**: 23-41.
- NIHLGÅRD (B.), 1971. — Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. *Oikos*, **22**: 302-314.
- NIHLGÅRD (B.), 1972. — Plant biomass, primary production and distribution of chemical elements in a beech and a planted spruce forest in South Sweden. *Oikos*, **23**: 69-81.
- OLSON (F.C.W.), 1950. — Quantitative estimates of filamentous algae. *Trans. Am. Microscop. Soc.*, **69**: 272-279.
- PARKINSON (D.), GRAY (T.R.G.) and WILLIAMS (S.T.), 1971. — *Methods for studying the ecology of soil micro-organisms*. IBP Handbook No 19. Blackwell Scientific Publications, Oxford, 116 p.
- PARKINSON (D.), DOMSCH (K.H.) and ANDERSON (J.P.E.), 1978. — Die Entwicklung mikrobieller Biomassen im organischen Horizont eines Fichtenstandortes. *Ecol. Plant.*, **13**: 355-366.

- SAITO (T.), 1955. — The significance of plate counts of soil fungi and the detection of their mycelia. *Ecol. Rev.*, **14**: 69-74.
- SKINNER (F. A.), JONES (P. C. T.) and MOLLISON (J. E.), 1952. — A comparison of a direct- and a plate-counting technique for the quantitative estimation of soil micro-organisms. *J. gen. Microbiol.*, **6**: 261-271.
- SÖDERSTRÖM (B. E.), 1975. — Vertical distribution of microfungi in a spruce forest soil in the south of Sweden. *Trans. Br. mycol. Soc.*, **65**: 419-425.
- SÖDERSTRÖM (B. E.), 1979a. — Some problems in assessing the fluorescein diacetate-active fungal biomass in the soil. *Soil Biol. Biochem.*, **11**: 147-148.
- SÖDERSTRÖM (B. E.), 1979b. — Seasonal fluctuations of active fungal biomass in horizons of a podzolized pine-forest soil in Central Sweden. *Soil Biol. Biochem.*, **11**: 149-154.
- STAAR (H.) and BERG (B.), 1977. — Mobilization of plant nutrients in a Scots pine forest mor in Central Sweden. *Silva Fennica*, **11**: 210-217.
- SWIFT (M. J.), 1973. — The estimation of mycelial biomass by determination of the hexosamine content of wood tissue decayed by fungi. *Soil Biol. Biochem.*, **5**: 321-332.
- VAN VEEN (J. A.) and PAUL (E. A.), 1979. — Conversion of biovolume measurements of soil organisms, grown under various moisture tensions, to biomass and their nutrient content. *Appl. Environ. Microbiol.*, **37**: 686-692.
- VISSER (S.) and PARKINSON (D.), 1975. — Fungal succession on aspen poplar leaf litter. *Can. J. Bot.*, **53**: 1640-1651.
- WIDDEN (P.) and PARKINSON (D.), 1973. — Fungi from Canadian coniferous forest soils. *Can. J. Bot.*, **51**: 2275-2290.